

Similar distribution pattern of different phenotypes of *Limnocythere inopinata* (Baird) in a brackish-water lake in Inner Mongolia

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Abstract It has been recognized long ago that *Limnocythere inopinata* is a widely distributed ostracod and comprises various phenotypes. The taxonomy of the different phenotypes and their ecological differences, however, are still under debate. In this study, we investigated the relationships between ostracod distribution, water depth, and the substrate based on the analyses of species composition, abundance, and age structure of ostracods in 51 surface-sediment samples from Dali Lake in Inner Mongolia in order to reveal the distribution pattern and habitat characteristics of the ostracods. The identification of a total of 32,182 valves indicates that the dominant ostracod in Dali Lake is *L. inopinata*, which includes unnodded, 1-, 2- and 3-node and 1-carina phenotypes. The distribution of *L. inopinata* is affected both by the water depth and by the sand content of the substrate, and the phenotypes show

their maximum abundances in the intermediate zone of the lake. All the phenotypes of *L. inopinata* display a similar preference for water depth and substrate, implying that the occurrence of different phenotypes is controlled by other factors. The age structure of *L. inopinata* is mainly related to the sand content, with the percentage of adults increasing and that of early juveniles decreasing with increasing sand content. Our data suggest that the occurrence of *L. inopinata* is closely related to water depth and substrate grain size, and different phenotypes of *L. inopinata* respond in a similar pattern to water depth and substrate.

Keywords Dali Lake · Surface sediment · Ostracod · Water depth · Substrate

Introduction

Ostracods, micro-crustaceans with calcite shells, usually colonize the bottom of oceans, lakes, swamps, and ponds. They exuviate eight times during their life and leave their shells in the sediments (Holmes, 2001). The occurrence of ostracods is closely related to the depth, temperature, salinity, and dissolved oxygen content of the water and the nature of the substrate (De Deckker, 1981; Benzie, 1989; Holmes, 2001), and the fossil shells thus provide ideal materials for studies of paleoenvironmental variations (Chivas et al., 1986; De Deckker & Forester, 1988; Horne & Mezquita, 2008).

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It is essential to investigate the ecology of extant ostracods in order to reconstruct paleoenvironmental conditions based on analyses of fossil ostracods. A number of investigations have been made to document the relation between the feature of ostracods and the physical and chemical properties of the ambient water (Külköylüoglu, 2004; Bunbury & Gajewski, 2005; Viehberg, 2006; Mischke et al., 2010). However, owing to the diversity of ostracods (Martens et al., 2008), and regional differences that may occur in the ecology of the same species across its range, our understanding of the response of ostracods to different environmental factors can only be improved if we undertake detailed studies of the morphology and age structure of single species in different lakes (Yin et al., 1999; Van Doninck et al., 2003). It is also important to examine concurrently ostracod species assemblages in the same lakes (Martín-Rubio et al., 2005).

Several datasets of extant ostracods record the ostracod assemblage of different lakes (e.g., Mezquita et al., 2005; Bunbury & Gajewski, 2005; Forester et al., 2005; Viehberg, 2006; Mischke et al., 2007), and from some of the databases, transfer functions of ostracod assemblages and environmental parameters (mainly water salinity and temperature) were established for quantitative paleoenvironmental reconstructions. It should be noted, however, that some datasets contain the ostracod assemblage recorded in a single sample from one lake. In reality the assemblages may be significantly different in different positions of a lake (Benzie, 1989; Martín-Rubio et al., 2005), implying that not any sample could be used to represent the ostracod assemblage of individual lakes. Therefore, the establishment of a high-quality database of extant ostracods needs a proper selection of the representative samples based on investigations of the within-lake distribution of ostracods in individual lakes.

In this study, 51 samples of the surface sediments of Dali Lake in central eastern Inner Mongolia were analyzed for ostracod assemblage, age structure of the dominant ostracod, and grain size. We attempt to investigate the spatial distribution of ostracods in the lake and then examine the relation between the ostracod assemblage and environmental factors. This study provides basic data both for understanding paleoenvironmental processes through the sedimentary sequence of Dali Lake and for selecting

representative samples from the lake for establishment of the extant ostracod database of lakes in northern China.

Study site

Dali Lake ($43^{\circ}13' \text{--} 23' \text{ N}$, $116^{\circ}29' \text{--} 45' \text{ E}$) is a closed-basin lake that lies 90 km west of Hexigten Banner, Inner Mongolia (Fig. 1). It has an area of 238 km^2 , a maximum water depth of 11 m, and an elevation of 1226 m above sea level. The lake sits at the northern margin of the W-E trending Hulandaga Desert Land and is surrounded by hills of basaltic rocks to the west, north, and east. Two permanent rivers from the northeast and two intermittent streams from the southwest feed the lake.

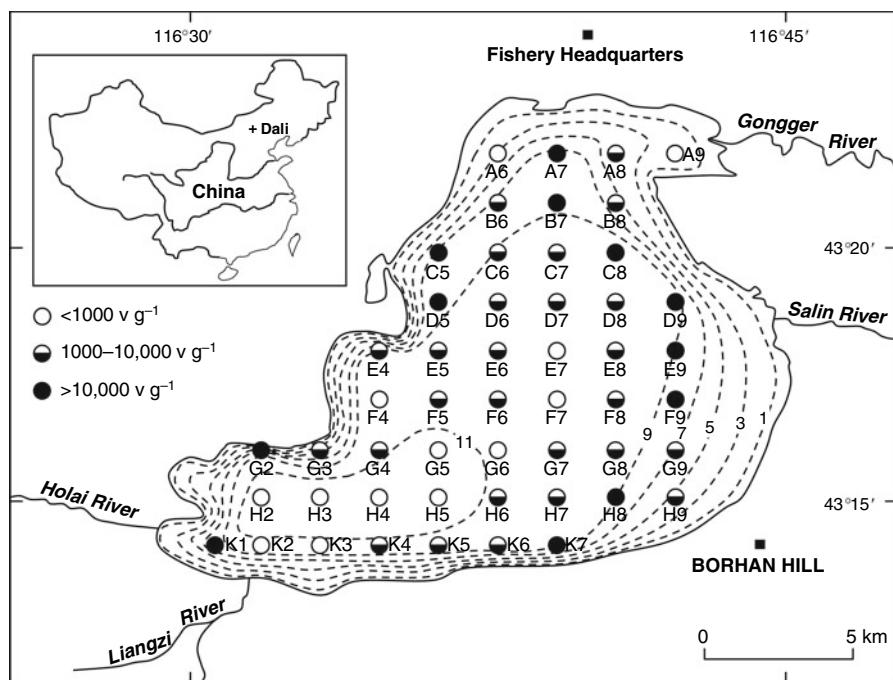
Dali Lake is located at the transition from semi-humid to semi-arid areas in the middle temperate zone of China (Chinese Academy of Sciences, 1984). In the lake region, mean annual temperature is $1\text{--}2^{\circ}\text{C}$ with a July average of $16\text{--}18^{\circ}\text{C}$ and a January average of -17 to -24°C . Mean annual precipitation is 350–400 mm with 70% of the annual precipitation falling in June–August. Mean annual evaporation reaches 1287 mm (Li, 1993). The lake is covered with ca. 1 m of ice from November to April (Li, 1993).

The modern natural vegetation of the Dali Lake region is categorized as temperate steppe and dominated by grasses (Li, 1993). Herbs of *Stipa grandis*, *Leymus chinensis*, and *Cleistogenes squarrosa* are distributed in the grasslands on the hills. Xeric plants of *Artemisia deuterorum*, *Polygonum divaricatum*, and *Agriophyllum squarrosum* grow in the Hulandaga Desert Land, accompanied by small patches of shrubs of *Salix gordeivii*, *Ulmus pumila*, and *Caragana sinica*.

The water of Dali Lake has a pH of 9.5 and a salinity of 5.6 g l^{-1} with major cations of $\text{Na}^+ + \text{K}^+$ (97.4%), Mg^{2+} (2.3%), and Ca^{2+} (0.3%) and major anions of Cl^- (40.1%), HCO_3^- (31.7%), CO_3^{2-} (21.8%), and SO_4^{2-} (6.4%) (Li, 1993). Aquatic plants are scarce in the lake and confined to the areas of the river mouth. The benthic fauna of the lake consists mainly of Gastropoda, Oligochaeta, Crustacea, and Insecta, and most of these animals inhabit the near-shore zone (Li, 1993).

The lake region is sparsely populated. Local people are engaged in animal husbandry and do not undertake any agricultural activity. A fishery unit was

Fig. 1 Map of Dali Lake showing sites of 51 samples from the surface sediments. Capital letters with numerals mark the sample numbers. Solid, half-solid, and hollow circles indicate the total abundance of ostracods in the samples. Dashed lines with numerals represent the bathymetry of the lake (contour in meters)



set up on the lakeshore (Fig. 1) in 1956 to organize fishery production. Fishery management activities have been carried out in winter since the 1970s to protect fish resources (Li, 1993).

Materials and methods

Surface-sediment sampling

The surface sediments of Dali Lake were sampled at intervals of 1 min of latitude (equivalent to 1.9 km) and 1.5 min of longitude (equivalent to 2 km) (Fig. 1), yielding 51 samples for laboratory analyses. Sediment cores were extracted in a 60- or 80-cm-long polyethylene tube using a gravity corer with a check valve on the top. The water–sediment interface and the top 2–3 mm of light-colored sediments are clearly discernible in the core tube, indicating that the uppermost part of the sediment core was accumulated during the most recent years. The top 1 cm of the core was cut for samples of the surface sediments after carefully siphoning the water in the core tube with a plastic pipe. The water depth of the sampling sites was measured with an FE-606 Furuno Echo Sounder.

Ostracod analysis

For each sample of ca. 100 mg of air-dried sediment, 60 ml of 10% H_2O_2 –0.1% Na_2CO_3 solution (pH 9–10) was added to disaggregate the sediment for 24 h. The resulting residue was sieved in water through a 250-mesh sieve with a pore size of 63 μm . The remains of the sample were rinsed repeatedly and spread onto a glass plate (9 cm \times 12 cm) as thin stripes with a buret (4-mm inner-caliber) and then dried in an oven at 40°C. All the ostracod shells including both living and dead individuals in the sample were identified and counted with an Olympus stereomicroscope.

Identification of the ostracods generally follows the taxonomy of Hou et al. (2002) and Hou & Gou (2007). Specimens of the genus *Limnocythere* with different numbers of nodes on their shell were, however, identified as different phenotypes of *Limnocythere inopinata* according to Yin et al. (1999) and Meisch (2000) rather than different species of *Limnocythere* as described by Hou & Gou (2007). In practice, specimens of *L. inopinata* >200 μm in length (generally 4–8th instars and adults) were grouped into unnoded, 1-, 2- and 3-node and 1-carina types, whereas those <200 μm (generally 1st–3rd instars)

were treated as a single unit because of the difficulty in micro-morphological observation.

Grain-size analysis

Grain-size distribution of the samples was determined with a Malvern Mastersizer 2000 laser grain-size analyzer. About 200 mg of sediment from each air-dried sample was pretreated with 10–20 ml of 30% H₂O₂ to remove organic matter and then with 10 ml of 10% HCl with the sample solution boiled to remove carbonates. About 2000 ml of deionized water was added, and the sample solution was kept for 24 h to rinse acidic ions. The sample residue was dispersed with 10 ml of 0.05 M (NaPO₃)₆ on an ultrasonic vibrator for 10 min before grain-size analysis. The Mastersizer 2000 has a measurement range 0.02–2000 µm in diameter and a grain-size resolution of 0.166 phi in interval, thus yielding 100 pairs of grain-size data. It automatically outputs the percentages of mud (<63 µm) and sand (63–2000 µm) fractions of a sample. Duplicate analyses of the same sample showed that the relative error of percentages of the related size fractions is less than 1%.

Numerical analyses

The ostracod abundance diagram of 51 samples was divided into ostracod assemblage zones based on cluster analysis (CONISS, Grimm, 1987). The program CANOCO version 4.5 (Ter Braak & Šmilauer, 2002) was used to ordinate the ostracod data from the surface sediments and to detect the pattern of spatial distribution of the ostracods and the relation between the ostracod assemblage and the environmental factors. Ostracod groups with abundances >30 v g⁻¹ (valves per gram) in at least one sample were used for ordination in this study, and a logarithmic transformation was applied to the data. Detrended correspondence analysis (DCA) showed that the gradient length of the first axis is 1.989, indicating a linear response of the ostracod assemblage to the environmental variables (Ter Braak & Šmilauer, 2002). Therefore, principal component analysis (PCA) and redundancy analysis (RDA) were chosen for ordination of the ostracod data and the environmental variables including the water depth and the sand content in the samples. The RDA

showed that the variance inflation factors (VIFs) for water depth and sand content are 2.344, much lower than 10, indicating a low collinearity between both environmental variables. In order to examine the effect of the water depth and the sand content on the ostracods separately, partial RDA was applied to the data on abundance and age structure (i.e., percentages of adults and juveniles <200 µm) of *Limnocythere inopinata*. In addition, linear regression was used to examine the heterogeneity in spatial distribution of ostracods at different water depths and different sand contents.

Results

Distribution of the ostracods

The surface sediments of Dali Lake contain abundant ostracods. Most samples yielded between 100–2000 ostracod valves, with a total of 32,182 valves from the 51 samples (Fig. 1). Six species of ostracods belonging to 6 genera were identified. These include *Limnocythere inopinata* (Baird), *Cytherissa lacustris* (Sars), *Candonia cf.houae* Huang, *Candoniella* sp., *Cypridopsis* sp., and *Ilyocypris bradyi* Sars with *L. inopinata* representing 99.7% of the total (Figs. 2, 3). In the population of *L. inopinata*, juveniles <200 µm comprise 44.6% of all individuals, whereas the unnoded, 1-, 2- and 3-node and 1-carina phenotypes account for 33.4, 6.1, 0.05, 15.9, and 0.02%, respectively. The unnoded and 3-node types, major phenotypes of *L. inopinata*, have adult female/male ratios of 4.4 (*n* = 322) and 4.8 (*n* = 233), showing no statistical difference (*P* = 0.66).

The ostracod abundance diagram plotted against water depth can be divided into 4 ostracod assemblage subzones based on CONISS: 1a (1.5–7.0 m), 1b (7.0–9.0 m), 2a (9.0–10.0 m), and 2b (10.0–11.5 m) (Fig. 3). All the phenotypes of *L. inopinata* display similar distributions. *L. inopinata* is less abundant in subzone 1a with an average abundance of 2847 v g⁻¹, but shows a trend of increases in the abundance with increasing water depth. In subzone 1b, *L. inopinata* reaches its highest abundance with an average of 16,342 v g⁻¹. It decreases dramatically in subzone 2a to an average abundance of 6092 v g⁻¹, and becomes scarce in subzone 2b and almost absent toward the deepest part of the lake.

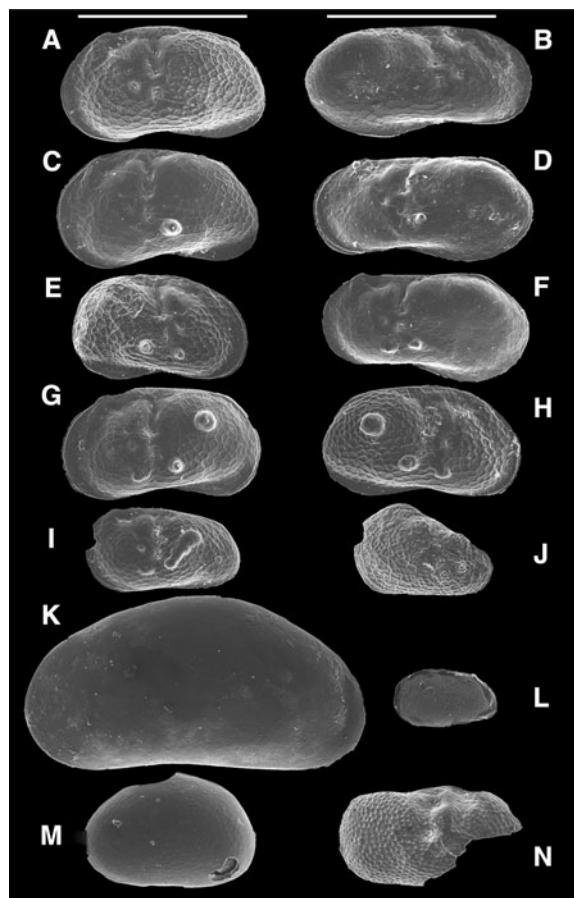


Fig. 2 Photos of ostracods in the surface sediments of Dali Lake, generated by a Leica S440i scanning electron microscope. (A) *Limnocythere inopinata* (Baird) (unnodded) female adult, left, 602×342 µm. (B) *L. inopinata* (unnodded) male adult, right, 670×329 µm. (C) *L. inopinata* (1 node) female adult, left, 598×353 µm. (D) *L. inopinata* (1 node) male adult, left, 648×310 µm. (E) *L. inopinata* (2 nodes) female adult, right, 519×311 µm. (F) *L. inopinata* (2 nodes) male adult, left, 612×320 µm. (G) *L. inopinata* (3 nodes) female adult, left, 587×331 µm. (H) *L. inopinata* (3 nodes) female adult, right, 586×325 µm. (I) *L. inopinata* (1 carina) female, late juvenile, left, 455×247 µm. (J) *Cytherissa lacustris* (Sars) juvenile, left, 410×274 µm. (K) *Candona cf. houae* Huang adult, left, 1009×515 µm. (L) *Candoniella* sp. juvenile, left, 306×170 µm. (M) *Cypridopsis* sp. late juvenile, right, 506×337 µm. (N) *Ilyocypris bradyi* Sars late juvenile, right, 544×298 µm. Scale = 500 µm

Among the rare species of the ostracods in Dali Lake, *C. lacustris*, *C. cf. houae*, and *Candona* spp. are relatively common (Fig. 3). These species appear frequently in subzones 1a and 1b, become scarce in subzone 2a, and disappear in subzone 2b.

Grain size of the substrates

All the samples from the surface sediments of Dali Lake consist of mud (<63 µm) and sand (63–2000 µm) and contain no gravels (>2000 µm). Such a grain-size distribution of the samples indicates that the content of the mud fraction in the samples has an absolutely negative relation to that of the sand fraction. In other words, the sand content in the samples increases while the mud content decreases. For this reason, only the sand content in the samples was used in this study to represent the characteristics of grain size of the substrates.

As shown in Fig. 3, sand content in the surface sediments decreases from the near-shore to the center of the lake. It ranges from 20 to 80% where water depth is less than 9 m and decreases to below 15% in the zone of deeper waters.

PCA analysis

Principal component analysis of major ostracod groups and samples from the surface sediments reflects the feature of the ostracod abundance diagram and the pattern of spatial distribution of the ostracods in Dali Lake (Fig. 4). The first and second axes capture 69.9 and 11.8% of the total variance within the ostracod data. The four clusters corresponding to the ostracod assemblage subzones are separated from each other on PCA biplot. Subzone 1a is characterized by 2-noded *L. inopinata*, *C. lacustris* and *C. cf. houae*; subzone 1b characterized by unnodded, 1- and 3-noded and juvenile *L. inopinata*, *Candona* spp., 2-noded *L. inopinata*, *C. cf. houae* and *C. lacustris*; subzone 2a characterized by unnodded, 1- and 3-noded and juvenile *L. inopinata*. Few ostracods characterize subzone 2b. Among the eight ostracod groups, unnodded and 1- and 3-noded *L. inopinata* and their juveniles display a similar distribution mainly in subzone 1b; whereas *Candona* spp., 2-noded *L. inopinata*, *C. lacustris* and *C. cf. houae* are similar in distribution in subzones 1b and 1a.

RDA, partial RDA, and linear regression analyses

Redundancy analysis of major ostracod groups and samples from the surface sediments reflects the relation between the ostracod assemblage and the

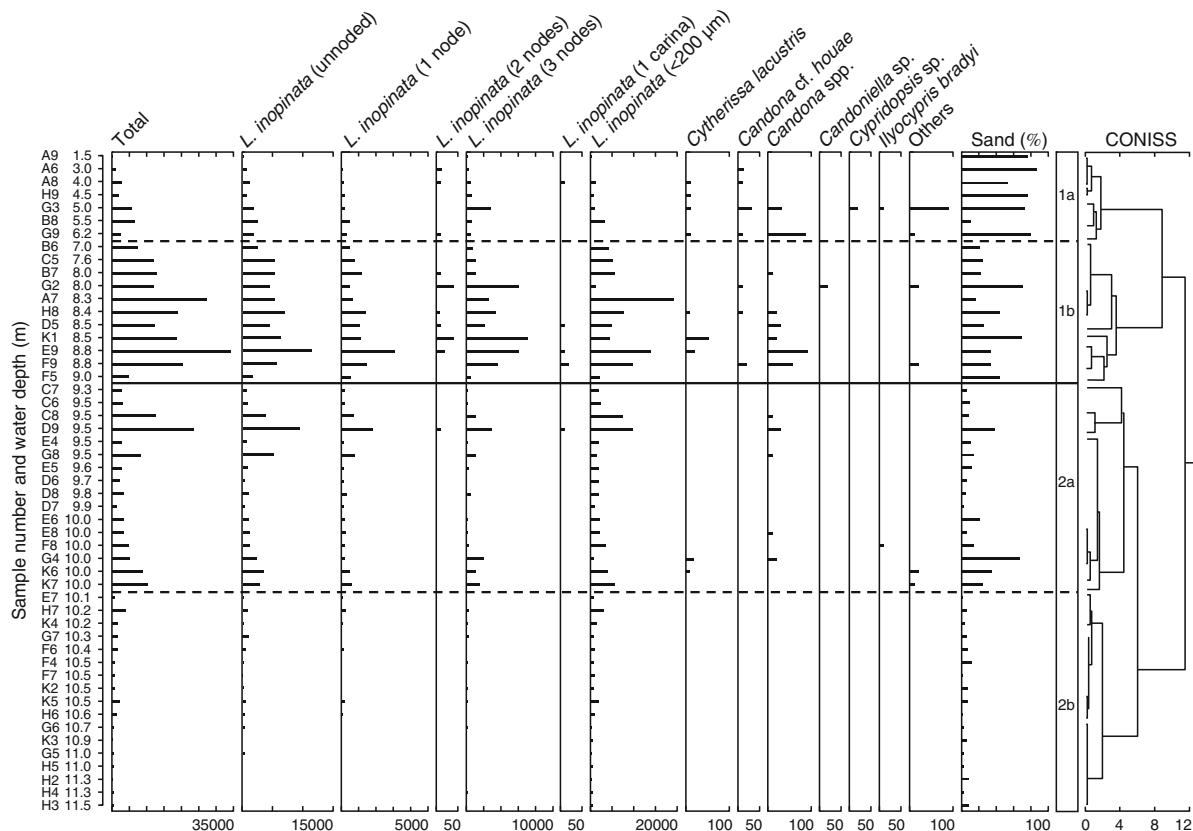


Fig. 3 Abundance ($v\ g^{-1}$) of the ostracods and content (%) of the sand fraction in 51 samples of the surface sediments of Dali Lake, plotted against water depth and sample number. Note

that the water depth is not linear and the samples are arranged in order of water depth. Cluster analysis (CONISS) is based on the total sum of squares ($\times 10^4$)

environmental variables (Fig. 5). The first and second axes capture 19.1 and 1.0% of the total variance within the ostracod data. Among the eight ostracod groups, *L. inopinata* juveniles lie in the negative direction of the sand content and the positive direction of the water depth; whereas the other seven groups all lie in the positive direction of the sand content and the negative direction of the water depth. It is noticeable that the unnoded and 1-, 2- and 3-noded phenotypes of *L. inopinata* are quite close to each other.

As all the phenotypes of *L. inopinata* have similar spatial distributions and relationships with environmental factors, *L. inopinata* is investigated as a whole with the analysis of partial RDA and linear regressions below.

Linear regressions demonstrate how the relationships between the abundance of *L. inopinata* and environmental factors vary according to water depth and different substrate. As shown in Fig. 6, the relation

between the *L. inopinata* abundance and the water depth and sand content in zone 1 is entirely different from that in zone 2. In zone 1, the *L. inopinata* abundance is related positively to the water depth and negatively to the sand content. In zone 2, however, it is related negatively to the water depth and positively to the sand content. Partial RDA suggests that the water depth and the sand content explain 50.9 and 27.8% of the variance of the *L. inopinata* abundance in zone 1 and 56.0 and 18.4% of the variance of the *L. inopinata* abundance in zone 2 (Table 1).

Moreover, the percentage of *L. inopinata* adults decreases with increasing water depth and increases with increasing sand content (Fig. 7). By contrast, the percentage of *L. inopinata* juveniles $<200\ \mu m$ increases with increasing water depth and decreases with increasing sand content (Fig. 8). Partial RDA indicates that, in zones 1 and 2, the sand content explains 49.0 and 26.1% of the variance of the *L. inopinata* age structure and the water depth explains

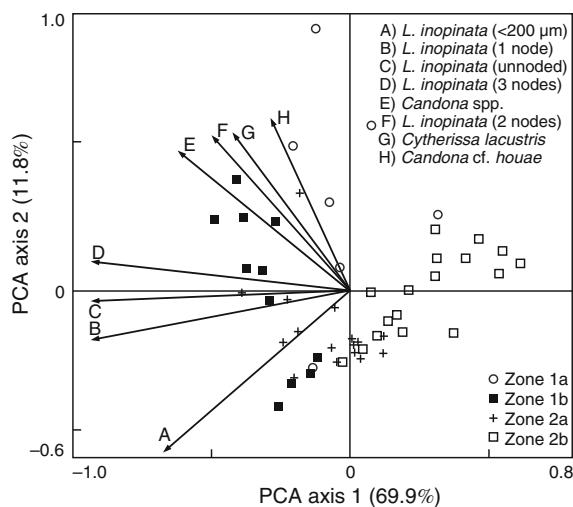


Fig. 4 PCA biplot of eight ostracod groups with abundances $>30 \text{ v g}^{-1}$ in at least one sample and the total ostracod data of 51 samples of the surface sediments of Dali Lake. Eigenvalues of the first and second axes are 0.699 and 0.118. The first and second axes capture 81.7% of the total variance within the dataset

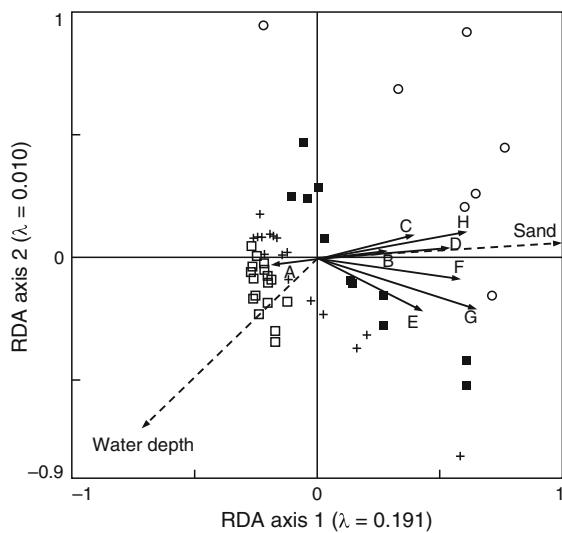


Fig. 5 RDA triplot of eight ostracod groups with abundances $>30 \text{ v g}^{-1}$ in at least one sample, the total ostracod data of 51 samples of the surface sediments of Dali Lake and two environmental variables (water depth and contents of sand fraction). For ostracod species labels (A–H) and sample symbols see Fig. 4

0.3 and 6.7% of the variance of the *L. inopinata* age structure (Table 2). The data imply that the water depth has a less significant effect on the age structure of *L. inopinata* either in zone 1 or in zone 2.

Discussion

Distribution of the ostracods and the environments

It was recognized long ago that some *Limnocythere* ostracods have different numbers of nodes on their shell. However, the taxonomy of *Limnocythere* with different nodes is still under debate. Yin et al. (1999) suggested that *Limnocythere* with different nodes could be classified as the same species, *Limnocythere inopinata*, based on the morphological and phylogenetic similarities of these ostracods. Meisch (2000) indicated that the morphological difference between *Limnocythere* with different nodes is well within the range of interspecific variations and proposed that these ostracods should be assigned as *Limnocythere inopinata*. In the meantime, Meisch (2000) put forward four phenotypes of *L. inopinata*, unnoded and 1-, 2- and 3-noded types, and gave a detailed description of the morphological features of these phenotypes. By contrast, Hou & Gou (2007) regarded *Limnocythere* with different nodes as different species in order to facilitate stratigraphical correlation based on fossil ostracods. Unnodded and 1-, 2- and 3-noded *Limnocythere* were given species names of *Limnocythere dubiosa* Daday, *Limnocythere sancti-patricii* Brady & Robertson, *Limnocythere binoda* Huang, and *Limnocythere inopinata* (Baird), respectively (Hou & Gou, 2007). In this study, *Limnocythere* with different nodes found from the surface sediments of Dali Lake were identified as different phenotypes of *L. inopinata* according to Yin et al. (1999) and Meisch (2000). It is noticeable that recent phylogenetic studies suggest that some classic ostracod species are actually species complexes comprising a great number of cryptic species with different DNAs (Bode et al., 2010). This finding implies that *L. inopinata* with different nodes may also be such a species complex (K. Martens, personal communication). In this study, however, it is difficult to view *L. inopinata* with different nodes as cryptic species because the identification of cryptic species is usually based on differences in DNA rather than morphology of ostracod species.

Although the morphological features of different phenotypes of *L. inopinata* have been described in detail (Meisch, 2000), the ecological significance of occurrence of the nodes remains unclear. Our data from Dali Lake suggest that all the phenotypes of

Fig. 6 **A** Plots of the relationships between the abundance of *L. inopinata* and the water depth and between the abundance of *L. inopinata* and the sand content in zone 1. **B** Plots of the relationships between the abundance of *L. inopinata* and the water depth and between the abundance of *L. inopinata* and the sand content in zone 2. All the *P*-values are less than 0.05, indicating significant linear regressions

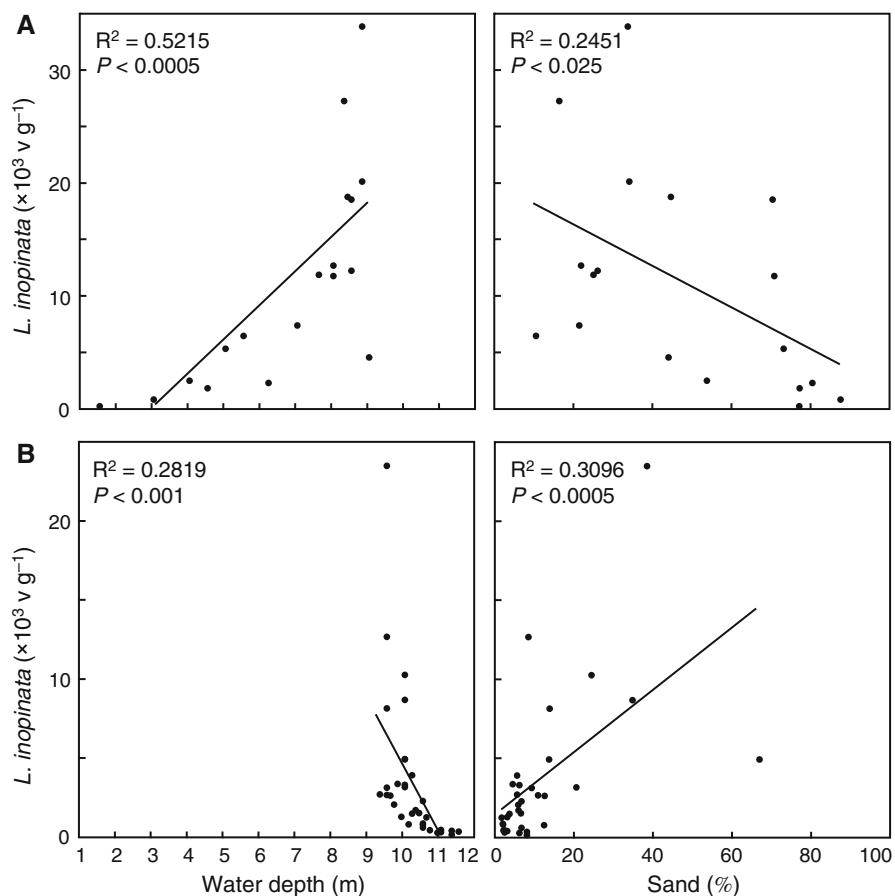


Table 1 Partial RDA of data of the *L. inopinata* abundance in zones 1 and 2

Zone	Variable	Covariable	λ_1	λ_1/λ_2	Significance (<i>P</i>)	Variance (%)
1	Depth	Sand	0.329	2.222	0.002	50.9
	Sand	Depth	0.123	0.831	0.004	27.8
2	Depth	Sand	0.432	2.171	0.002	56.0
	Sand	Depth	0.077	0.387	0.002	18.4

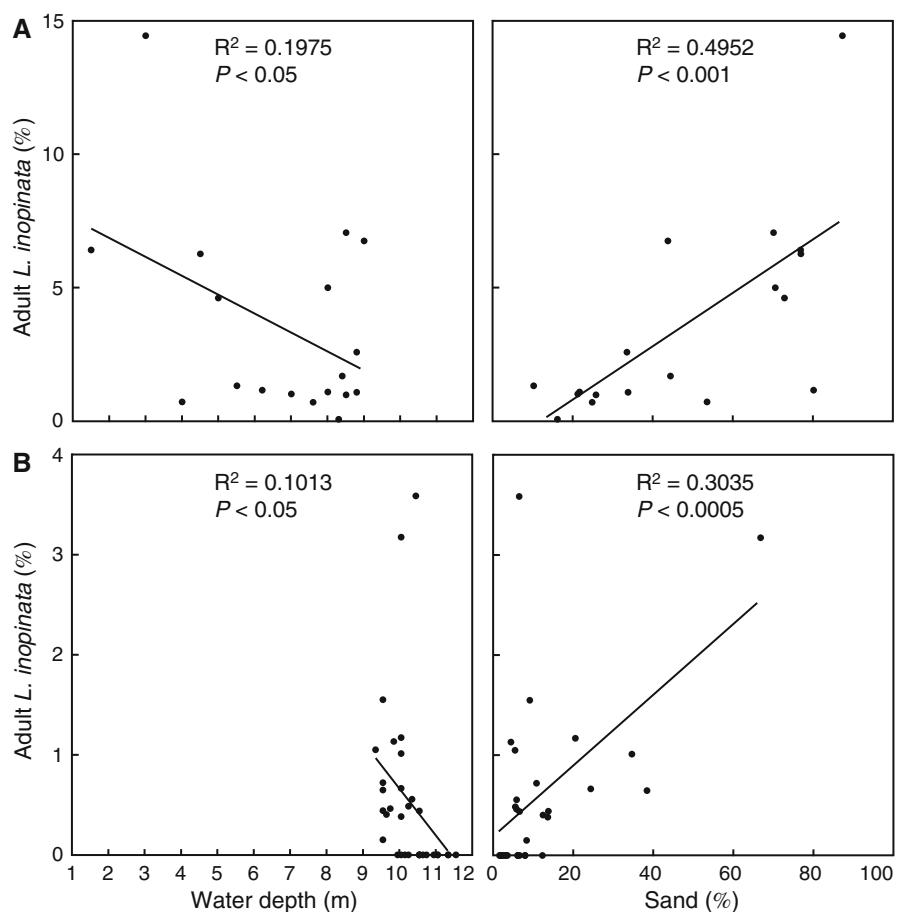
The water depth and the sand content are used as variable or covariable separately. All the *P*-values are less than 0.05, indicating significant influences of both the water depth and the sand content

L. inopinata have a similar preference both for depth of water and sand content of substrate. All the phenotypes of *L. inopinata* are most abundant at depths of 7.0–9.0 m, less abundant at depths of 9.0–10.0 m and 1.5–7.0 m, and scarce at depths of 10.0–11.5 m (Fig. 3). In respect of the substrate grain size, they all prefer sandy substrates to muddy ones (Fig. 5). Based on these data, we infer that the occurrence of different phenotypes of *L. inopinata* is determined by factors other than water depth or

substrate grain size. Ostracods exuviate 8 times all through their life and their shells are made up of calcite. Taking these characteristics into consideration, occurrence of the phenotypes is most probably related to the salinity of waters (Zhang et al., 2006), the genetics of ostracods (Yin et al., 1999), or a combination of both. Further investigations are needed to solve this mystery.

Previous investigations indicate that the distribution of *L. inopinata* in lakes is closely associated to

Fig. 7 **A** Plots of the relationships between the percentage of adult *L. inopinata* and the water depth and between the percentage of adult *L. inopinata* and the sand content in zone 1. **B** Plots of the relationships between the percentage of adult *L. inopinata* and the water depth and between the percentage of adult *L. inopinata* and the sand content in zone 2. All the *P*-values are less than 0.05, indicating significant linear regressions



the content of organic matter in the substrate and the coverage of aquatic plants on the lake floor. In Lake Neusiedlersee on the Austria–Hungary border, *L. inopinata* is much more abundant in the western part of the lake, where organic matter is rich in the sediments, than in the other part (Jungwirth, 1979). In Lake Strathbeg in northeast Scotland, *L. inopinata* was found to prefer bare substrates to vegetated ones (Benzie, 1989). In the case of Dali Lake, the spatial distribution of *L. inopinata* is affected both by the water depth and by the sand content in the substrate. It reaches the highest abundance in the intermediate zone between the near-shore area and the lake center where both the water depth and the sand content are at a moderate level. Based on these data, we suggest that the within-lake distribution of *L. inopinata* could be influenced by varied environmental factors such as water depth, contents of organic matter and sand in the substrate, and aquatic plants on the lake floor.

The less abundant species in Dali Lake, *C. lacustris*, *C. cf. houae*, and *Candona* spp., exhibit both ecological similarities to, and differences from, the dominant species, *L. inopinata* (Figs. 3, 4). All the species of the ostracods in the lake have a preference for sandy substrates. As for water depth, the rarer species appear frequently both in subzone 1b and 1a, whereas *L. inopinata* occurs mostly in subzone 1b.

The ostracods in Dali Lake show poor diversity and low abundance where water is more than 10 m deep. This feature can also be seen in other lakes, such as Lake Banyoles (Riera & Roca, 1995) and Lake Caiuso de Yuso (Martín-Rubio et al., 2005) in Spain. In Lake Banyoles, ostracods are absent in the profundal zone, which was attributed to oxygen shortage (Riera & Roca, 1995). In Lake Caiuso de Yuso, ostracods become scarce in the zone where water depth was greater than 10 m and

Fig. 8 **A** Plots of the relationships between the percentage of juvenile ($<200 \mu\text{m}$) *L. inopinata* and the water depth and between the percentage of juvenile ($<200 \mu\text{m}$) *L. inopinata* and the sand content in zone 1. **B** Plots of the relationships between the percentage of juvenile ($<200 \mu\text{m}$) *L. inopinata* and the water depth and between the percentage of juvenile ($<200 \mu\text{m}$) *L. inopinata* and the sand content in zone 2. All the *P*-values are less than 0.05, indicating significant linear regressions

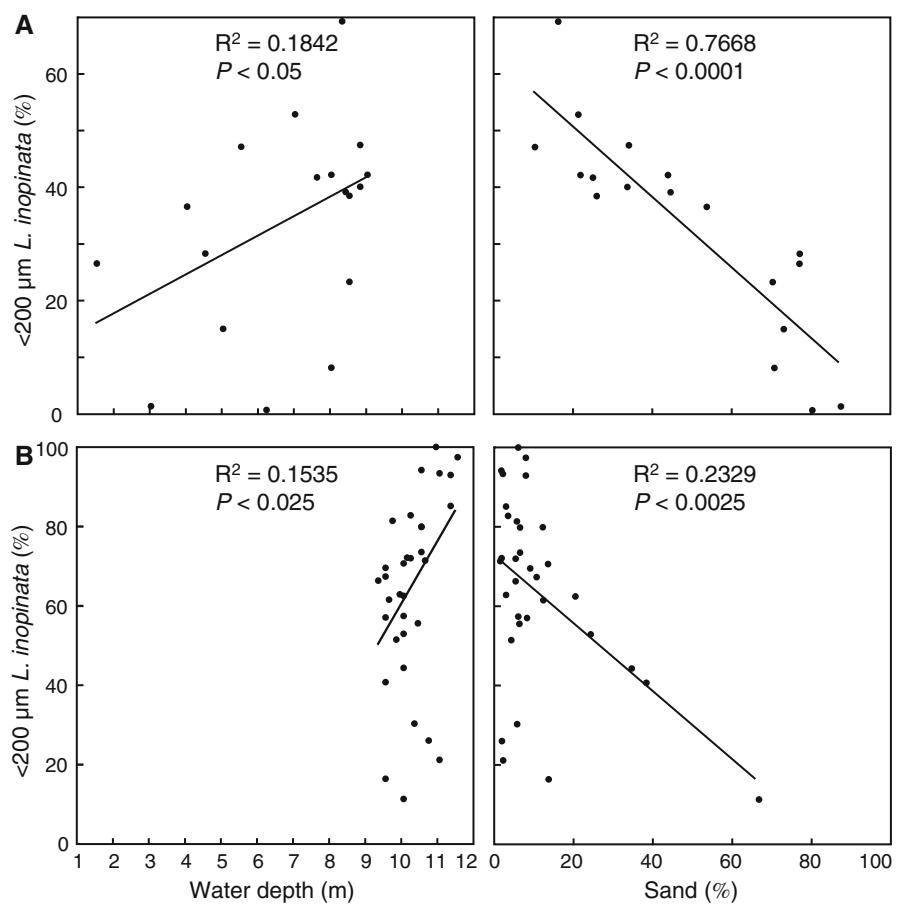


Table 2 Partial RDA of data of adult and juvenile ($<200 \mu\text{m}$) *L. inopinata* percentages in zones 1 and 2

Zone	Variable	Covariable	λ_1	λ_1/λ_2	Significance (<i>P</i>)	Variance (%)
1	Depth	Sand	0.002	0.007	0.940	0.3
	Sand	Depth	0.417	1.381	0.002	49.0
2	Depth	Sand	0.046	0.108	0.124	6.7
	Sand	Depth	0.228	0.536	0.014	26.1

The *P*-values indicate a significant influence of the sand content ($P < 0.05$) and an insignificant influence of the water depth ($P > 0.05$)

the scarcity of ostracods was thought to result from the decreased oxygen content and the increased carbon dioxide content in the lake bottom waters (Martín-Rubio et al., 2005). We thus speculate that the reduced number of ostracods in the deep-water zone of Dali Lake could be related to reduced oxygen and/or lower pH of the waters. On the other hand, the low abundance of ostracods in the lake center may reflect the occurrence of high lake levels in view of the absence of the rarer species from this area.

Age structure of *L. inopinata* and the environments

The age structure of *L. inopinata* in Dali Lake displays a significant spatial pattern of an older population in the near-shore zone and a younger one in the offshore zone. Linear regressions suggest that the age structure of *L. inopinata* is seemingly related both to the water depth and to the sand content (Figs. 7, 8). When the effect of other variables is

excluded, however, the partial RDA indicates that the sand content has a much greater influence on the age structure of *L. inopinata* than the water depth both in zones 1 and 2 (Table 2). These data imply that the relation between the age structure and the water depth shown in Figs. 7, 8 might have resulted from the relation between the water depth and the sand content rather than from the response of the age structure to the water depth. With respect to the possible mechanism responsible for the relation between the age structure of *L. inopinata* and the sand content, the following three points can be considered.

First of all, the adults and juveniles of *L. inopinata* may have different preferences of the substrate, i.e., the former prefer coarser substrates and the latter prefer finer substrates. Such being the case, the adults would represent a large proportion of *L. inopinata* in sandy substrates, whereas the juveniles would constitute the majority of *L. inopinata* in muddy substrates.

On the other hand, the adults and juveniles of *L. inopinata* may be different in their adaptability to hydraulic disturbances. The ostracods of the genus *Limnocythere* are accustomed to calm waters because they are typically crawling ostracods and unable to swim (Colin & Danielopol, 1978; Meisch, 2000). We assume that *L. inopinata* of different ages have different abilities to resist the scouring of wave action. If adults are better able to resist hydraulic disturbances than the juveniles are, there would be more adults in sandy substrates and more juveniles in muddy substrates because higher sand contents in the substrates of the near-shore zone is associated with the higher hydraulic energy of the shallow waters.

Finally, the process of post-mortem transportation probably from the littoral area to the deeper part of the lake might alter the age structure of *L. inopinata* because of its different sizes at different stages. It was suggested that post-mortem transportation would have occurred if certain ages of shells were absent from the mortem ostracod assemblage because the reworking process of the mortem could result in the removal of either the adults or the earlier instars from the original mortem (Whatley, 1988). In other words, the effect of within-lake transportation of ostracod shells would be negligible if the ostracod assemblages contain both the adults and the juveniles. As shown in Figs. 7 and 8, most of the samples from Dali Lake comprise the adults and the earlier instars of *L. inopinata*, presumably implying an insignificant

influence of the transporting and re-depositing processes within the lake to the ostracod distribution. In any case, further investigations are needed to understand the mechanism responsible for the within-lake difference in the age structure of *L. inopinata*.

Representative ostracod samples from individual lakes

A regional database of the occurrence of extant ostracods based on the ostracod samples from a number of lakes does not only provide vital information on the geographical occurrence of ostracods in different lakes (Mezquita et al., 2005; Forester et al., 2005) but also contributes to a better understanding of the migration and evolution of animals (Horne & Martens, 1999). Special attention should thus be paid to the representativeness of the ostracod samples from individual lakes to improve the reliability of regional ostracod database.

Bunbury & Gajewski (2005) suggested that samples taken from the lake center would be representative of the ostracods in the lake because the lake center is an area receiving materials from the whole lake. Therefore, they took samples from the central part of 36 lakes in Yukon and British Columbia of western Canada to establish the database of the extant ostracods. By contraries, Viehberg (2006) took samples from the near-shore zone of 33 lakes in northeast Germany for the establishment of a regional ostracod database. In the case of Dali Lake, however, both a high abundance and a great diversity of the ostracods occur neither in the lake-center zone nor in the near-shore zone but in the intermediate zone (water depths: 7–9 m). We therefore suggest that ostracod samples should be collected from the intermediate zone to obtain data representative of the ostracods in Dali Lake. This is necessary to guarantee both a sufficient quantity of the shells and full faunal information about the ostracods present.

To establish the ostracod database of North America, Forester et al. (2005) collected samples both from the near-shore zone and from the offshore zone of lakes. We concur with Forester et al. that ostracod samples used for a regional database should be taken from different zones of lakes if possible. As the ostracod assemblage may be different from part to part within a lake, a proper selection of the ostracod samples representative of an individual lake based on

investigations on the spatial distribution of the ostracods is necessary. The representativeness of ostracod samples from individual lakes would contribute to the improvement of reliability of the regional ostracod database.

Conclusions

The ostracod assemblage of Dali Lake is dominated by *L. inopinata*, which has several phenotypes present. All the phenotypes of *L. inopinata* have a similar preference for the water depth and the substrate grain size, indicating that the occurrence of different phenotypes is controlled by other factors rather than water depth or substrate grain size. The distribution of *L. inopinata* is affected both by the water depth and by the sand content in the substrate. And the age structure of *L. inopinata* is related closely to the sand content but not to the water depth. Our data suggest that the representative ostracod samples from individual lakes would contribute to the improvement of reliability of the regional ostracod database.

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References

- Benzie, J. A. H., 1989. The distribution and habitat preference of ostracods (Crustacea: Ostracoda) in a coastal sand-dune lake, Loch of Strathbeg, north-east Scotland. Freshwater Biology 22: 309–321.
- Bode, S. N. S., S. Adolfsson, D. K. Lamatsch, M. J. F. Martins, O. Schmit, J. Vandekerckhove, F. Mezquita, T. Namotko, G. Rossetti, I. Schön, R. K. Butlin & K. Martens, 2010. Exceptional cryptic diversity and multiple origins of parthenogenesis in a freshwater ostracod. Molecular Phylogenetics and Evolution 54: 542–552.
- Bunbury, J. & K. Gajewski, 2005. Quantitative analysis of freshwater ostracode assemblages in southwestern Yukon Territory, Canada. Hydrobiologia 545: 117–128.
- Chinese Academy of Sciences (Compilatory Commission of Physical Geography of China), 1984. Physical Geography of China: Climate. Science Press, Beijing: 1–30 (in Chinese).
- Chivas, A. R., P. De Deckker & J. M. G. Shelley, 1986. Magnesium content of non-marine ostracod shells: a new palaeosalinometer and palaeothermometer. Palaeogeography, Palaeoclimatology, Palaeoecology 54: 43–61.
- Colin, J.-P. & D. L. Danielopol, 1978. New data on the systematics of the Limnocytheridae (Ostracoda, Cytheraceae). Geobios 11: 563–567.
- De Deckker, P., 1981. Ostracods of athalassic saline lakes. Hydrobiologia 81: 131–144.
- De Deckker, P. & R. M. Forester, 1988. The use of ostracods to reconstruct continental palaeoenvironmental records. In De Deckker, P., J.-P. Colin & J.-P. Peypouquet (eds), Ostracoda in the Earth Sciences. Elsevier, Amsterdam: 175–199.
- Forester, R. M., A. J. Smith, D. F. Palmer & B. B. Curry, 2005. North American Non-Marine Ostracode Database “NANODE” Version 1, Kent State University, Kent, OH, USA [available on internet at <http://www.kent.edu/NANODE>].
- Grimm, E. C., 1987. CONISS: a FORTRAN 77 program for stratigraphically constrained cluster analysis by the method of incremental sum of squares. Computers & Geosciences 13: 13–35.
- Holmes, J. A., 2001. Ostracoda. In Smol, J. P., H. J. B. Birks & W. M. Last (eds), Tracking Environmental Change Using Lake Sediments. Volume 4: Zoological Indicators. Kluwer Academic Publishers, Dordrecht: 125–151.
- Horne, D. J. & K. Martens, 1999. Geographical parthenogenesis in European non-marine ostracods: post-glacial invasion or Holocene stability? Hydrobiologia 391: 1–7.
- Horne, D. J. & F. Mezquita, 2008. Palaeoclimatic applications of large databases: developing and testing methods of palaeotemperature reconstruction using nonmarine ostracods. Senckenbergiana lethaea 88: 93–112.
- Hou, Y. T. & Y. X. Gou, 2007. Fossil Ostracoda of China, Vol. 2. Science Press, Beijing (in Chinese).
- Hou, Y. T., Y. X. Gou & D. Q. Chen, 2002. Fossil Ostracoda of China, Vol. 1. Science Press, Beijing (in Chinese).
- Jungwirth, M., 1979. *Limnocythere inopinata* (Baird) (Cytheridae, Ostracoda): its distribution pattern and relation to the superficial sediments of Neusiedlersee. In Löffler, H. (ed.), Neusiedlersee: The Limnology of a Shallow Lake in Central Europe. Junk, The Hague: 385–388.
- Külköylüoğlu, O., 2004. On the usage of ostracods (Crustacea) as bioindicator species in different aquatic habitats in the Bolu region, Turkey. Ecological Indicators 4: 139–147.
- Li, Z. G., 1993. Annals of Hexigten Banner. People’s Press of Inner Mongolia, Hohhot: 97–104, 547–555 (in Chinese).
- Martens, K., I. Schön, C. Meisch & D. J. Horne, 2008. Global diversity of ostracods (Ostracoda, Crustacea) in freshwater. Hydrobiologia 595: 185–193.
- Martín-Rubio, M., J. Rodríguez-Lazaro, P. Anadón, F. Robles, R. Utrilla & A. Vázquez, 2005. Factors affecting the distribution of recent lacustrine Ostracoda from the Cai-cedo de Yuso-Arreo Lake (Western Ebro Basin, Spain). Palaeogeography, Palaeoclimatology, Palaeoecology 225: 118–133.
- Meisch, C., 2000. Freshwater Ostracoda of Western and Central Europe. Spektrum Akademischer Verlag, Heidelberg.
- Mezquita, F., J. R. Roca, J. M. Reed & G. Wansard, 2005. Quantifying species–environment relationships in non-marine Ostracoda for ecological and palaeoecological studies: Examples using Iberian data. Palaeogeography, Palaeoclimatology, Palaeoecology 225: 93–117.

- Mischke, S., U. Herzschuh, G. Massmann & C. J. Zhang, 2007. An ostracod-conductivity transfer function for Tibetan lakes. *Journal of Paleolimnology* 38: 509–524.
- Mischke, S., U. Bößneck, B. Diekmann, U. Herzschuh, H. J. Jin, A. Kramer, B. Wünnemann & C. J. Zhang, 2010. Quantitative relationship between water-depth and sub-fossil ostracod assemblages in Lake Donggi Cona, Qinghai Province, China. *Journal of Paleolimnology* 43: 589–608.
- Rieradevall, M. & J. R. Roca, 1995. Distribution and population dynamics of ostracodes (Crustacea, Ostracoda) in a karstic lake: Lake Banyoles (Catalonia, Spain). *Hydrobiologia* 310: 189–196.
- Ter Braak, C. J. F. & P. Šmilauer, 2002. CANOCO Reference Manual and CanoDraw for Windows User's Guide: Software for Canonical Community Ordination (Version 4.5). Microcomputer Power, Ithaca.
- Van Doninck, K., I. Schön, K. Martens & B. Goddeeris, 2003. The life-cycle of the asexual ostracod *Darwinula stevensoni* (Brady & Robertson, 1870) (Crustacea, Ostracoda) in a temporate pond. *Hydrobiologia* 500: 331–340.
- Vieberg, F. A., 2006. Freshwater ostracod assemblages and their relationship to environmental variables in waters from northeast Germany. *Hydrobiologia* 571: 213–224.
- Whatley, R. C., 1988. Population structure of ostracods: some general principles for the recognition of palaeoenvironments. In De Deckker, P., J.-P. Colin & J.-P. Peypouquet (eds), *Ostracoda in the Earth Sciences*. Elsevier, Amsterdam: 245–256.
- Yin, Y., W. Geiger & K. Martens, 1999. Effects of genotype and environment on phenotypic variability in *Limnocythere inopinata* (Crustacea: Ostracoda). *Hydrobiologia* 400: 85–114.
- Zhang, L., Z. C. Sun, Z. S. An, W. G. Liu & X. Z. Li, 2006. A preliminary distribution analysis on Ostracoda of different water bodies from Qinghai Lake area, NW China. *Acta Micropalaeontologica Sinica* 23: 425–436 (in Chinese).